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IIASA Interim Report
July 2009

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Interim Report **IR-09-064**

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June 2010

Evolution of cooperation on dynamical graphs

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Abstract

There are two key characteristic of animal and human societies: (1) degree heterogeneity, meaning that not all individual have the same number of associates; and (2) the interaction topology is not static, i.e. either individuals interact with different set of individuals at different times of their life, or at least they have different associations than their parents. Earlier works have shown that population structure is one of the mechanisms promoting cooperation. However, most studies had assumed that the interaction network can be described by a regular graph (homogeneous degree distribution). Recently there are an increasing number of studies employing degree heterogeneous graphs to model interaction topology. But mostly the interaction topology was assumed to be static. Here we investigate the fixation probability of the cooperator strategy in the prisoner's dilemma, when interaction network is a random regular graph, a random graph or a scale-free graph and the interaction network is allowed to change.

We show that the fixation probability of the cooperator strategy is lower when the interaction topology is described by a dynamical graph compared to a static graph. Even a limited network dynamics significantly decreases the fixation probability of cooperation, an effect that is mitigated stronger by degree heterogeneous networks topology than by a degree homogeneous one. We have also found that from the considered graph topologies the decrease of fixation probabilities due to graph dynamics is the lowest on scale-free graphs.

Keywords: Game Theory; Prisoner's Dilemma; fixation probability; scale free network

Introduction

While cooperative behaviour is widespread in nature (Dugatkin, 1997), the mechanisms behind its evolution and maintenance are still not fully explored. Population structure has been proposed as one of the mechanism promoting cooperation (Nowak, 2006; Nowak and Sigmund, 2000). Until recently, most studies assumed that the interaction network can be described by a regular graph, which is indeed the case if the players are spatially confined. Ohtsuki *et al.* (2006) have shown for a number of other interaction topologies that selection favours cooperation (i.e. the fixation probability of a single cooperator is higher than the fixation probability of a neutral mutant) in the prisoner's dilemma game if the benefit (b) of the altruistic act divided by its cost (c) exceeds the average number of neighbours (k), that is, if $b/c > k$. They found this relation to be approximately valid if they use the so called "death-birth" update rule (details see below) in populations of different structure, in which interaction topology is described variously by regular, random regular, random, or scale-free graphs. Recently, Taylor *et al.* (2007) have proved mathematically that this relation is approximately valid for bi-transitive graphs. Furthermore similar relationship can be derived considering inclusive fitness (Lehman et al., 2007).

Both Ohtsuki *et al.* (2006) and Taylor and Nowak (2006) have assumed that the graph is static during evolution. This assumption implies that a newborn individual (or accepted strategy-by-imitation) in a given position interacts with exactly the same individuals that were connected to every preceding individual at this position. Dispersal from the natal patch (mostly by males) is widespread in Nature. Furthermore animal social structure exhibits both rapid changes and long term association (e.g. bottlenose dolphins (Connor et al., 1999); sperm whales (Whitehead, 1995; Whitehead, 1997); long-finned pilot whale (Ottensmeyer and Whitehead, 2003)). Dynamic social connection is characteristic of fission-fusion societies (e.g. chimpanzee (Mitani et al., 2002); spider monkey (Ramos-Fernández, 2005); onager and Grevy's zebra (Sundaresan et al., 2007); African buffalo (Cross et al., 2005); African elephant (Couzin, 1996)). As social networks are not static, the effect of assuming static interaction topology clearly needs attention. Parallely, some recent papers studied the evolution of cooperation on dynamical networks. They either studied the fixation probability of a single cooperator among defectors in the case when graph dynamics is much faster than the dynamics of evolution (Pacheco et al., 2006a), or if the relative speed of graph and evolutionary dynamics were varied systematically they assumed that cooperators and

defectors were in the same fraction initially in the population (Pacheco et al., 2006b; Santos et al., 2006a).

Here we investigate how sensitive is the fixation probability of a single cooperator to the network dynamics, if graph dynamics is slow relative to the evolution.

Methods

In order to allow comparison we considered the same methodology as in Ohtsuki et al. (2006). Namely, a population is considered where the interactions are described by a graph that can vary in time. The population of $N = 100$ [1] individuals consist of defectors and cooperators. An individual derives its payoff, P from interactions with adjacent individuals. A cooperator helps all individuals to whom it is connected, thus it pays a cost (c) for each of its neigbour. Neigbours of a cooperator receive the benefit (b). Generally, if a cooperator is connected to k other individuals and i of those are cooperators, then its payoff is $bi - ck$. A defector does not provide any help, and therefore has no costs, but it can receive the benefit from neighbouring cooperators. If a defector is connected to j cooperators, then its payoff is bj. The fitness of the a player is given by $\Phi = 1 - w + wP$, where w measures the intensity of the selection. Here we assume weak selection where the payoff is small compared to the baseline fitness ($w \ll 1$). (Other possibility is to normalize P by the number of neighbours of the individuals. In this case the beneficial effect of graph degree heterogeneity disappears (Santos and Pacheco, 2005; Szolnoki et al., 2008)

Following Ohtsuki *et al*. (2006) we employed a "death-birth" updating scheme, where at each update a randomly chosen individual dies; and subsequently the neighbours compete for the empty site in proportion to their fitness. Accordingly, the probability that neighbour i occupies the emptied site is $\Phi_i \Big/ \sum_{j=1}^{k_i} \Phi_j$, where the fitness of all neighbours are summed. (Alternatively three other update rules can be considered, which is called "birth-death", "imitation" and "pairwise comparison" (for details see Ohtsuki and Nowak, 2006). By using "death-birth", "imitation" or "pairwise comparison" rules evolution of the cooperative strategy is probable if b/c is high enough. However, "birth-death" updating rule has been demonstrated to be detrimental to the evolution of cooperation very close to the ones gained

1 (Ohtsuki *et al.* (2006) have also simulated a population of $N = 500$ individuals, with similar results as for $N = 100$, thus the use of smaller population is justified.

from a well mixed population (see e.g. Ohtsuki and Nowak, 2006; Ohtsuki and Nowak, 2008; Ohtsuki et al., 2007).

We have considered three different graph topologies: random regular graphs, random graphs and scale-free graphs. In each case the mean connectivity of the graphs (k) were varied. The graphs were generated as in Ohtsuki *et al.* (2006), although there are other methods of generating the employed graphs, but we wanted our results to be directly comparable to one of the most eminent prior study in this field. For *random regular graphs* (RRG), the links between nodes are randomly drawn under the constraint that every node ends up with an equal number of links, k. In order to ensure connectedness of the network, every node is first linked to a random node of the already connected ones. *Random graphs* (RG) are generated in much the same way as RRG, but relaxing the constraint that every node has the same number of links to having k links on average. As for RRG, we first need to make sure that the graph is connected. In a second step two randomly drawn nodes are linked. The second step is repeated until kN links have been distributed. *Scale-free networks* are generated according to the method of preferential attachment (Albert and Barabási, 2002).

The interaction network was allowed to change. After each update, ω fraction of the edges belonging to the site being updated was changed. The edge between the focal site and a randomly selected neighbour was exchanged with the edge connecting a randomly chosen site to its neighbour. For example, if A and B, and C and D, were originally connected, then after the update, A is connected to C, and B is connected to D. Because the number of edges belonging to a site never changes, the edge distribution of the graphs remain unchanged (Farkas et al., 2004; Maslov and Sneppen, 2002; Xulvi-Brunet et al., 2003).

In numerical simulations, we then measured the fixation probability of a single cooperator at different levels of graph dynamics (ω), different average numbers of neighbours (k), and variations in the benefit to cost ratio (b/c). The initial cooperator was placed in a randomly chosen node. For each parameter combination we have constructed 1000 graphs, and on each graph the simulation was repeated 1000 times. The total number of repetitions (n) was thus one million. We computed the number of cases (n_C) when the single cooperator spreaded and fixated in the population. Thus we estimated the average fixation probability $p_C = n_C / n$. Fixation of the cooperative strategy is supported if this probability is higher than the fixation of a neutral mutant, that is if $p_C = 1/n$.

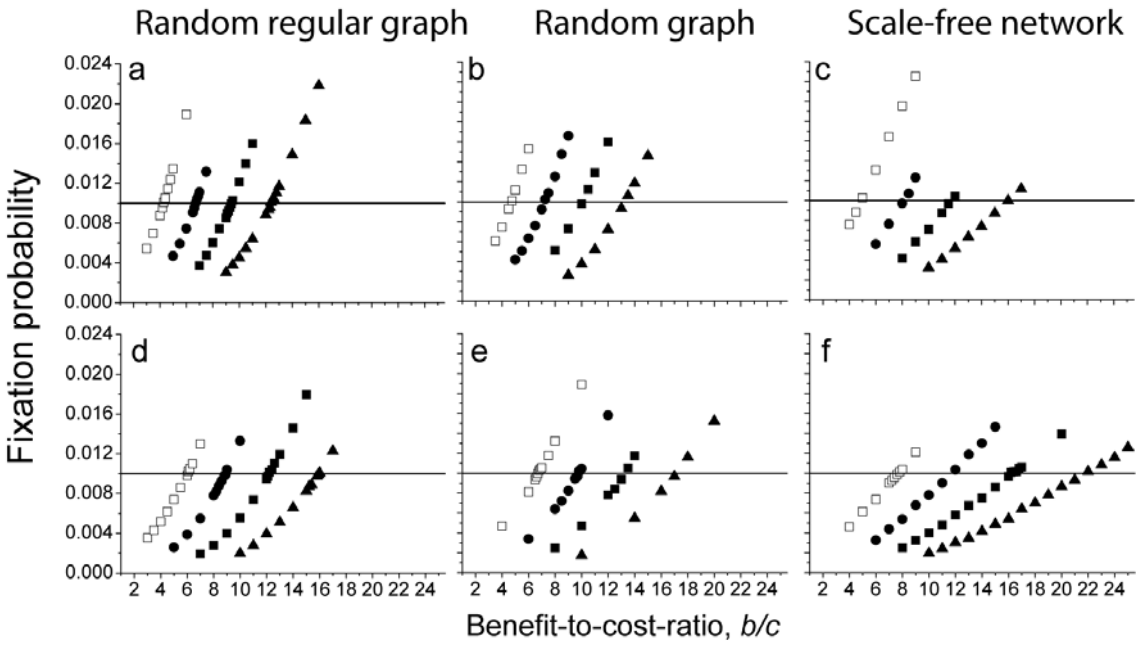

Figure 1 - Fixation probabilities of a single cooperator on static graphs (a-c) and on dynamic graphs (d-f), as a function of the benefit-to-cost ratio.

Mean number of neighbours (k) is 4 (open squares), 6 (circles), 8 (filled squares) or 10 (upward triangles). Graph dynamics in (d-f) are set to $\omega = 0.1$. The strength of selection is $w = 0.01$ in all cases.

Results

Numerical simulations show that the fixation probability of a cooperator is clearly lower than in the corresponding static graph model, even if the graph dynamics are set to be slow (Fig 1). The slower the dynamics the bigger the speed of decrease in fixation probability, indicating the sensitivity the results of Ohtsuki *et al.* (2006) to the assumption of static graphs (Fig 2). For example, while the $b/c > k$ relation is roughly valid for the static random-regular, and random graphs, it changes approximately to $b/c > (3/2)\ k$, even if only 10% of the newborn individual's connections change randomly (Fig 1.d and e). Interestingly decreasing of fixation probabilities with increasing graph dynamics is less intense if the interaction structure is described by a scale-free graph comparing to either the random or the random regular graph (Fig. 1.c and f). Naturally, it remains still valid that increasing b/c and decreasing k increases the fixation probability of cooperator.

Edge swapping cannot be implemented in regular graphs. Instead, individuals were exchanged to simulate changes in the interaction network (which is not edge swapping *per se*). Here again, we found that fixation probabilities decreased rapidly with increasing graph dynamics (data not shown). Thus, changes in the interaction network have the same

qualitative effect as in the other graphs, even though direct comparison of the regular graph with the others is not possible.

Discussion

We found that dynamics in the interaction network lowers the fixation probability of the cooperative strategy. It is trivial that in the limit of very fast network dynamic we arrive at the well mixed case, where defection is the only ESS. This limit could have been reached in a qualitatively different way. For example fixation probability drops significantly only at very high values of network dynamic, or it may decrease linearly with increasing network dynamics. These were found to be not the cases, as even a very small amount of dynamic decreased fixation probability significantly. Thus, studying static graphs might lead us to the conclusion that the evolution of cooperation is easy. However, it is not the case in the more realistic setting, where the interaction network is changing, and the linking dynamic is slow and linking is not preferential.

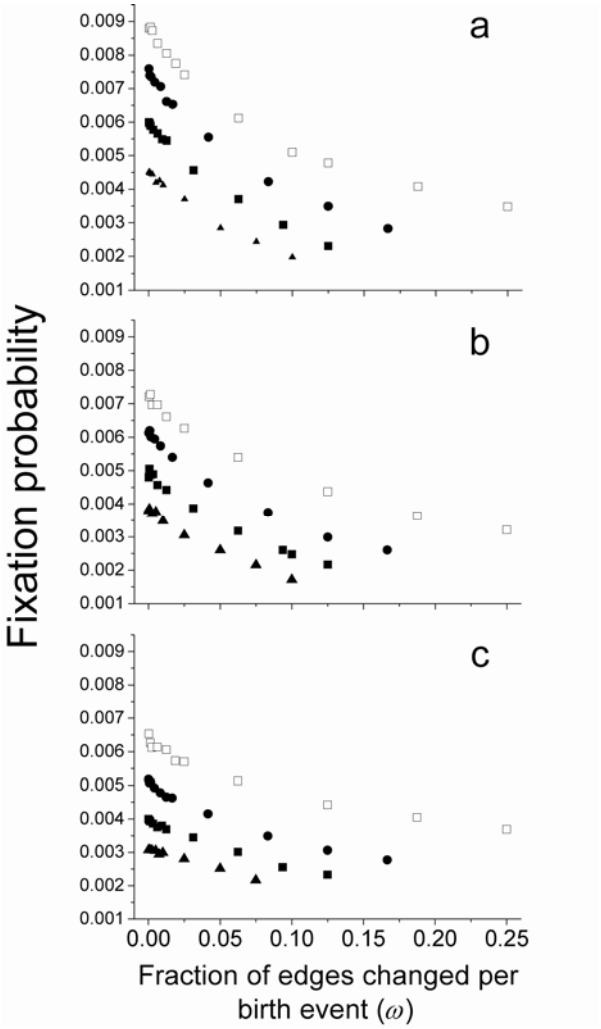

Figure 2. Fixation probabilities of a single cooperator on dynamic graphs as a function of the intensity of graph dynamics. Mean number of neighbours (k is 4 (open squares), 6 (circles), 8 (filled squares) or 10 (upward triangles). Graph dynamics in (d-f) are set to ω = 0.1. The strength of selection is w = 0.01 and b/c=k in all cases.

In our investigation the network dynamics was slow and the relinking random. The rate of link change was comparable to the rate of deaths and births of individuals. We employed these slow rates to show that even this causes significant effect. There is evidence that stable association that only change with death and birth do exist in nature (e.g. Karczmarski et al., 2005). This can serve as a base line: there is always some topological change in the interaction network, it cannot be static. Because in most cases generations are overlapping,

parents and offspring cannot have exactly the same interaction topology, thus graph dynamic is always present. And even if generations are non-overlapping the environmental fluctuations and stochastic demography will cause change in interaction topology. However, we can ask whether frequency of change in interaction is under evolution? Our results suggest that having zero graph dynamic is evolutionarily more favourable, than having any other amount, assuming that graph topology has not changed and rewiring of graph is random. However, as stated above, this state cannot be realized. Still, the frequency of interaction change is under evolutionarily pressure. However, most of these pressures are not associated with cooperation. For example in fission-fusion societies, interaction network changes, for example, because of temporal change of available food (chimpanzees: Lehmann and Boesch, 2004; Lehmann et al., 2007; African elephants: Wittemeyer et al., 2005; zebras: Rubenstein and Hack, 2004). Thus there is selection pressure on the behaviour producing fission and the subsequent fusion of the groups.

We employed random relinking in order to focus on the effect of network change. A behaviour which selectively aborts interaction with cheaters and/or search the partnership of cooperators can have positive fitness consequences. Active linking has been shown to benefit cooperation (Pacheco et al., 2006a), but there are two effects in play: that of network change, and that of the preferential choice of individuals to create or to break links with others. Here we have shown that network dynamic alone is harmful to cooperation, and thus we infer that active linking can mitigate its effect (this will be studied in an upcoming paper). The detrimental effect of randomness in partnership was demonstrated by Vukov and Szabó (2004) for a spatial PD with voluntary participation (i.e. there is a third strategy, the Loner besides Cooperation and Defection (Szabó and Hauert, 2002)). In their model a small fraction of the links in the regular network is temporarily replaced by random links. They have found that cooperation decreases with increased randomness in the system, and even a very small amount (around 8%) of randomization results in loss of the cooperating strategy (Vukov and Szabó, 2004).

We have shown that from the considered graph topologies the decrease of fixation probabilities due to graph dynamics is the lowest on scale-free graphs (Fig. 1). Degree heterogeneity is the highest on the scale-free graph among the employed graphs, and mean fixation probability at a given b/c is the lowest on such graphs (Fig. 1). We have found that fixation probability increased with the degree of the first cooperator node.

Interestingly, a power law distribution was found to describe human cooperation networks (Barabási, 2002; Ebel et al., 2002; Smith, 2002). Lusseau (2003) found scale-free behaviour for large connectivities in a social network of bottlenose dolphins. While population sizes are usually smaller than required for indicating a scale-free degree distribution in social associations, some facts suggest that the structure of animal association network might resemble these graphs. Associations are not random, and certain individuals act as hubs for the society. Older females are identified as hubs in bottlenose dolphins (Lusseau, 2003) and in African elephants (McComb et al., 2001). It seems that certain pigs are more "popular" than others (Durell et al., 2004), an observation which was also made for other domestic animals. Spotted hyenas females tend to associate more with higher ranking females (Smith et al., 2007). Degree heterogeneity seems to be common in animal societies; and it promotes cooperation (Santos et al., 2006b). Here we have shown that the scale-free network structure buffers the effect of change in association, which is always present in the network.

Acknowledgements

We are grateful for the comment of Szabolcs Számadó on earlier draft of the manuscript. Á.K. was a postdoctoral fellow of OTKA (D048406) and currently is a Lisa Meitner Postdoctoral Fellow (M983-N18). I.S. acknowledges support from the Hungarian Research Funds (OTKA T049692, TECT-OTKA NN71700).

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